

## ECOLOGICAL PHYSIOLOGY OF LARVAL EUPHAUSIIDS, *EUPHAUSIA SUPERBA* (EUPHAUSIACEA)

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Studies of the effects of environmental variability on the physiology of the early life history stages of the Antarctic krill, *Euphausia superba*, suggest that there are several critical periods during the first year of life that will affect survival, and thus recruitment of young krill into the adult population. The first critical period occurs during development of the non-feeding stages. Results of a collaborative modelling study suggest that release of embryos over warm deep water (250–400 m) is advantageous for these early larval stages. The geographical distribution of spawning populations combined with the observed pattern in sinking rates of embryos during development form a reproductive strategy that maximises survival of the early non-feeding stages. The first winter is the second critical period. Physiological condition (condition factor, lipid content, and growth rate) of larvae and juveniles is an index of their nutritional history and ability to survive and enter the adult population the following summer. Significant differences were found in the physiological condition of larvae collected during two winters which differed primarily in the degree of ice cover. Larvae in the heavy ice winter had higher growth rates, higher condition factor and more lipid. Although phytoplankton in the water column were scarce in both winters, ice biota were an additional possible source of food during the heavy ice winter. □ *Larval euphausiids, reproductive strategy, recruitment, physiological condition, critical period.*

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The most abundant euphausiid in the world's oceans, *Euphausia superba* Dana, the Antarctic krill, lives only in the Southern Ocean. This one species is often the dominant herbivore, unlike the case in most other oceans where copepods are the important grazers of phytoplankton primary production (Clarke, 1985). Although Antarctic krill have a circumpolar distribution, high concentrations are found in only a few locations (Marr, 1962; Laws, 1985).

Because krill are concentrated within the area of strong seasonal variation in pack ice cover, many investigators have postulated a close coupling between sea ice and krill populations due to associated food sources (Laws, 1985; Quetin and Ross, 1991). Sea ice provides a habitat in which microscopic plants and animals can live and grow. In addition fresh water from melting sea ice in the spring promotes water column stability and ice-edge blooms of phytoplankton several months before the open water blooms (Smith *et al.*, 1988). The annual advance and retreat of sea ice involves about 16 million km<sup>2</sup> of ocean surface, advancing from a minimum of 4 million km<sup>2</sup> in summer to a maximum of more than 20 million km<sup>2</sup> in late winter (Garrison and Siniff, 1986).

Growth and reproductive cycles of krill are

keyed to the extreme seasonal cycle of primary production in the Antarctic caused by lack of light in the fall and winter (Quetin and Ross, 1991). Phytoplankton concentrations in the water column are also very low during these periods (0.1 to 0.2 µg chl a l<sup>-1</sup> (Ross *et al.*, 1987; McClatchie, 1988)). Krill are long-lived for a pelagic crustacean, with an estimated maximum life span of seven or eight years (Ettershank, 1984; Siegel, 1987; Berman *et al.*, 1989). They probably begin to reproduce in their third summer. Although the ovary begins to mature in September and October, embryos are not released until the summer months, unlike most other Antarctic zooplankton that spawn in the spring. *E. superba* releases multiple batches of embryos throughout the spawning season if food supplies are sufficient (Ross and Quetin, 1983, 1986; Cuzin-Roudy, 1987). Spawning intensity will thus depend on regional environmental conditions. Once released, krill embryos sink rapidly out of the surface layers, hatching at 600 to 1000 m after 4.5 to 6 days (Marschall and Hirche, 1984; Quetin and Ross, 1984; Ross and Quetin, 1985). The newly hatched larvae then begin their ascent to the surface. The nonfeeding naupliar stages are usually found below 250 m, but Calyptopsis 1 (C1), the first

larval stage with a mouth and feeding appendages, are usually found in the lighted surface layer with their food source – phytoplankton (Marschall, 1985). Embryos released in mid- to late December appear in the surface layers as Calyptopsis I in early to mid-January, about the same time as the summer phytoplankton bloom. Thus, production of embryos and larvae is timed so C1s usually encounter food once they arrive at the surface. Larval developmental times through the three calyptopsis and six furcilia stages depend on temperature and food availability. Estimates range from four months with excess food (Ikeda, 1985) to 10–11 months (mid-November) under winter conditions of low food and temperatures (Ross *et al.*, 1987; Elias, 1990).

*Euphausia superba* is a 'keystone' species in the Antarctic food web. Because of their high biomass and long life span, Antarctic krill provides a year-round food source. In fact they are often the primary food source for predators in this ecosystem (Laws, 1985). Turnover rates and recruitment success of *E. superba* are of particular interest because of its integral role in the dynamics of the Antarctic ecosystem and the possible impact of the commercial fishery for krill.

Fisheries researchers have long recognised that there are periods during early larval life that are critical to survival and to the recruitment success or failure of the year class (Hjort, 1914; May, 1974). More recently the same concept has been applied to crustacean larvae (Anger and Dawirs, 1981; Dawirs, 1987; Ross and Quetin, 1989). Identification of these critical periods and the possible consequences will allow us to predict variability in recruitment success from pertinent environmental factors.

In this paper we describe recent research that focuses on several factors that influence inter-annual variability in recruitment success of *E. superba*. By recruitment we mean the abundance of the age class 1+, the youngest subadults, at the beginning of their second summer. Clearly both reproductive output of adults, termed 'recruitment potential', and survival of the embryos and larvae impact the size of the year class, and are the sources of annual and geographical variability in recruitment. We will focus on two studies relevant to the success of early life history stages. Each study identifies one critical period in the first year of life. The approaches used avoid several of the logistical and theoretical problems inherent in sampling a mobile species with an ocean-wide and patchy distribution (Hamner *et*

*al.*, 1983, 1984; Kanda *et al.*, 1982). These approaches yield valuable insight into recruitment dynamics and population maintenance, and are valuable techniques for those wishing to understand processes underlying variability in recruitment of other pelagic crustaceans.

The first study is a coupled biological/physical model that integrates laboratory measurements of the physiology and behaviour of the embryos and non-feeding larval stages and the actual vertical temperature structure of the waters near the Antarctic Peninsula (Hofmann *et al.*, in press). The objective was to simulate the descent/ascent cycle under different environmental conditions to explore questions about the relative success of spawning in different hydrographic regimes. The second study documents the effects of inter-annual variability in winter conditions on the physiological condition and thus survival of larvae and juveniles during their first winter (Quetin *et al.*, in press). Results from these two studies have helped us understand how environmental variability can lead to success or failure of a year class in *E. superba*.

#### DESCENT/ASCENT MODEL OF EARLY LIFE HISTORY

The first critical period in *E. superba*'s life history occurs during the descent/ascent cycle immediately after release of the embryo. Because the embryos and early larvae depend solely on internal reserves until C1 (Quetin and Ross, 1989), the reserves remaining at metamorphosis to C1 is a function of environmental temperature and its effect on metabolism and development. From our laboratory studies of starvation tolerance during this first feeding stage, we know that the point-of-no-return (PNR) ranges from 10 to 14 days (Ross and Quetin, 1989). After the PNR, even if food does become available, larvae are unable to recover from the effects of prolonged starvation. They fail to develop normally and eventually die. Thus the level of initial reserves, how fast they are used, and whether food is available shortly after the C1 reaches the surface determine larval success in this first critical period.

#### TIME- AND TEMPERATURE-DEPENDENT MODEL

A time- and temperature-dependent model (Hofmann *et al.*, in press) was developed to answer several questions relevant to the use of internal reserves in the embryos and early larvae: (1) how do water mass characteristics affect the use of reserves?, (2) what are the hatching depths

and thus the depth from which the larvae have to ascend?, and (3) what reserves are still available when the larvae reach the surface? The model simulates the descent/ascent physiology and behaviour of embryo and early larval stages under different hydrographic conditions.

Development and definition of parameters of the model included careful consideration of the biology and physiology of the embryos and larvae of *E. superba*. Temperature affects developmental and metabolic rates (Ross *et al.*, 1988; Quetin and Ross, 1989), and also has a direct effect on the survival of the early life history stages. Embryos and larvae reared at  $-1^{\circ}\text{C}$  do not continue development past the C1 stage (Ross *et al.*, 1988). We suggest that there may be a temperature sensitive period at some point during early development, and that a necessary developmental process does not take place at negative temperatures. Older stages survive and grow at these low temperatures, so we believe that it is only very early in development that exposure to low temperatures has deleterious effects. We also incorporated the effects of temperature and developmental stage on larval ascent rates (Ross *et al.*, 1985).

Because sinking rates of the embryos are critical to hatching depths, one important aspect of the model was to simulate the sinking rate pattern of the embryos during development (Quetin and Ross, 1984; Ross and Quetin, 1985). Changes observed in sinking rates imply changes in the density of the embryo during development. Initially embryos sink rapidly,  $175$  to  $200$   $\text{m d}^{-1}$ . After about 24 h, however, sinking rates decrease to  $50$  to  $60$   $\text{m d}^{-1}$ . Just prior to hatching, sinking rates increase to near initial rates. The sinking rate pattern was clear. What was not clear was whether this pattern was important in the life cycle of Antarctic krill, and what, if any advantages such a pattern would confer on the species. High initial velocities serve to remove embryos from schools of feeding adult krill, a probable predator, but the advantages of the subsequent decrease in sinking rates were not apparent.

With the model we derived depth profiles of the embryo and larva, and calculated the decrease in carbon during development under different temperature regimes. The simulated descent and ascent patterns are primarily a result of the effect of temperature on the developmental times of early life history stages. Development in *E. superba* is equiproportional, i.e. each developmental stage occupies the same proportionate amount of time relative to other

stages at any constant temperature (Ross *et al.*, 1988). Because development in Antarctic krill is equiproportional, the biological processes included in the model are formulated in terms of fraction of total developmental time (Hofmann *et al.*, in press).

#### SIMULATIONS

Simulations of the descent/ascent cycle were run for constant temperatures and for actual vertical profiles from the waters west of the Antarctic Peninsula, particularly at locations around the South Shetland Islands and in the Bransfield Strait (Hofmann *et al.*, in press). In some parts of this region warm Circumpolar Deep Water (CDW), warmer than  $0^{\circ}\text{C}$ , is found between 200 and 600 m (Fig. 1). Except for seasonal warming of the surface waters, waters above and below the CDW are less than  $0^{\circ}\text{C}$ .

Simulations with constant temperatures show the role of temperature in determining the depth of hatching and the total time for the descent/ascent cycle (Hofmann *et al.*, in press). Longer developmental times affect the total sinking period and the time at high sinking rates. In addition, larvae swim more slowly at colder temperatures and have to ascend from deeper water, increasing the use of energy reserves before reaching the surface. Over deep cold water embryos hatch at depths  $>1000$  m, and metamorphose to C1 within the lighted surface layer. At warmer temperatures krill larvae reach the surface well before metamorphosis into the first feeding stage, so have a longer time at the surface to find food before passing the PNR. However, even at  $-1^{\circ}\text{C}$  less than 20% of the total carbon was used during the descent/ascent cycle (Hofmann *et al.*, in press), far less than the 50% level for the PNR (Ross and Quetin, 1989).

The simulations show that under no conditions do larvae pass the PNR before reaching the surface. However, if the underlying water is cold, larvae arrive at the surface with less time before they need to feed.

Simulations of the descent/ascent cycle with observed vertical temperature structures emphasised the role of temperature in controlling the hatching depth, the time spent on the bottom before hatching, and the amount of carbon used during the cycle (Hofmann *et al.*, in press). In regions characterised by warm CDW at depth, such as north of the South Shetland Islands where water warmer than  $0^{\circ}\text{C}$  is found at all depths greater than 150 m, embryos arrive in waters greater than  $1^{\circ}\text{C}$  about 1.5 d after release.

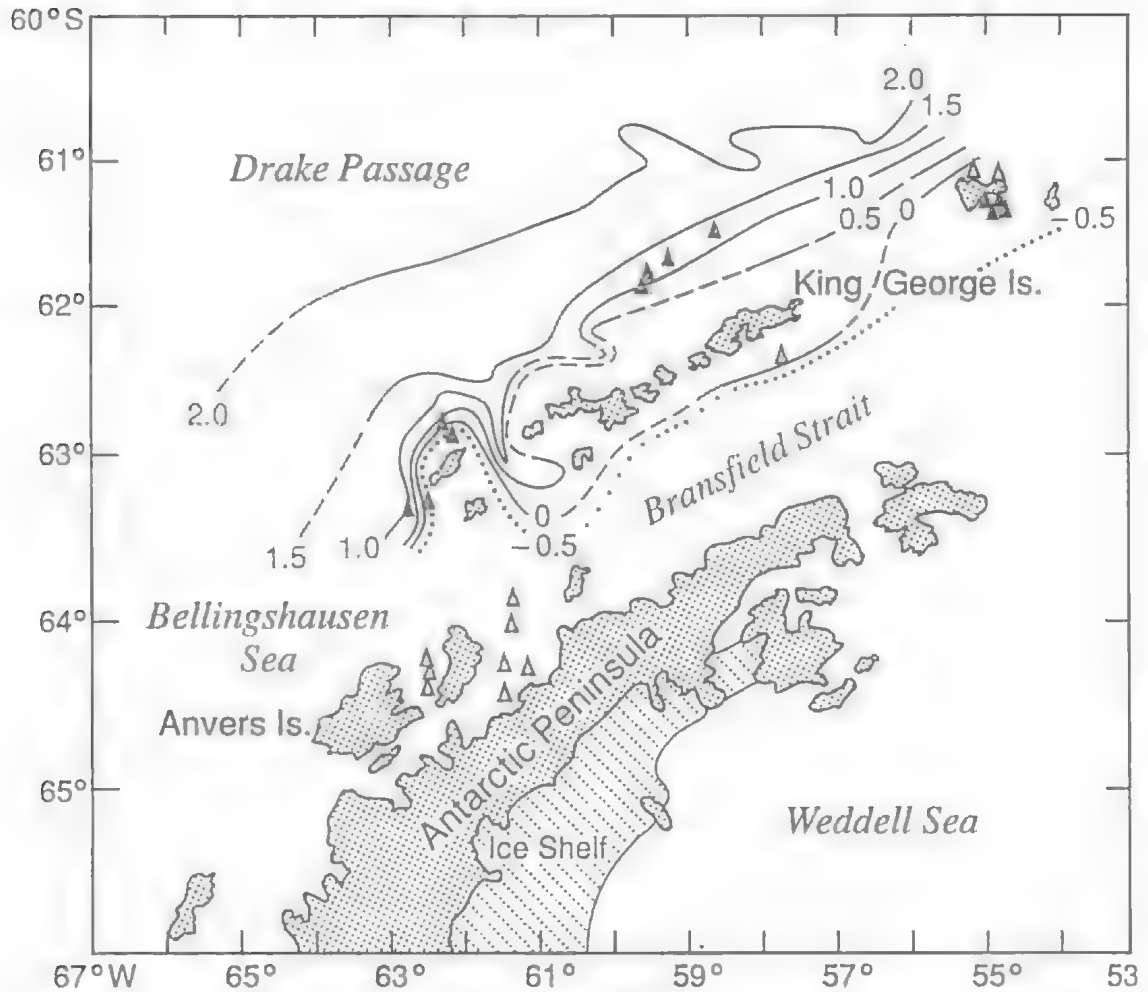


FIG. 1. Composite temperature distribution at 500 m in area of study. The distributions were constructed using historical temperature data collected during the last ten years from XBT and CTD observations. Contour interval is 0.5°C. Dashed lines indicate extrapolation of the temperature (data from Hofmann *et al.*, in press). Distributions of krill schools in 1982 containing gravid ( $\blacktriangle$ ) and nonreproducing females ( $\triangle$ ) are plotted (Quetin and Ross, 1984).

Because sinking rates are very low during the few days, embryos remain in this CDW until hatching, about 5 d after release and at 680 m (Fig. 2a). In the eastern Bransfield Strait, waters are less than  $-1^{\circ}\text{C}$  at all depths. Hatching time is almost 10 days. Slower developmental times mean that the period of high initial sinking rates lasts longer, and embryos reach about 500 m before slowing down. Embryos hit bottom at 1000 m 2 days before hatching, and about 20% of embryonic development occurs on the bottom (Fig. 2b). In contrast embryos released north of the Shetland Islands hatch before they reach bottom. North of the South Shetland Islands, larvae complete their ascent in about 13 days,

bringing the total descent/ascent cycle to 18 days. Total carbon use is about  $2\ \mu\text{g C}$ , 13% of initial values (Fig. 2c). Ascent rates in the eastern Bransfield Strait, however, are slower so larvae take about 25 days to complete the ascent, for a total descent/ascent time of 35 days, about twice as long as in the area north of the South Shetland Islands (Fig. 2d). Total carbon use throughout the descent/ascent cycle is about 26% of the initial carbon content of the embryo, again twice as much as for the area over CDW. This carbon usage brings the larvae much closer to the PNR of  $7.5\ \mu\text{g C}$ , or a 50% decrease, and gives the larvae fewer days in which to find food.

These simulations show firstly that embryos



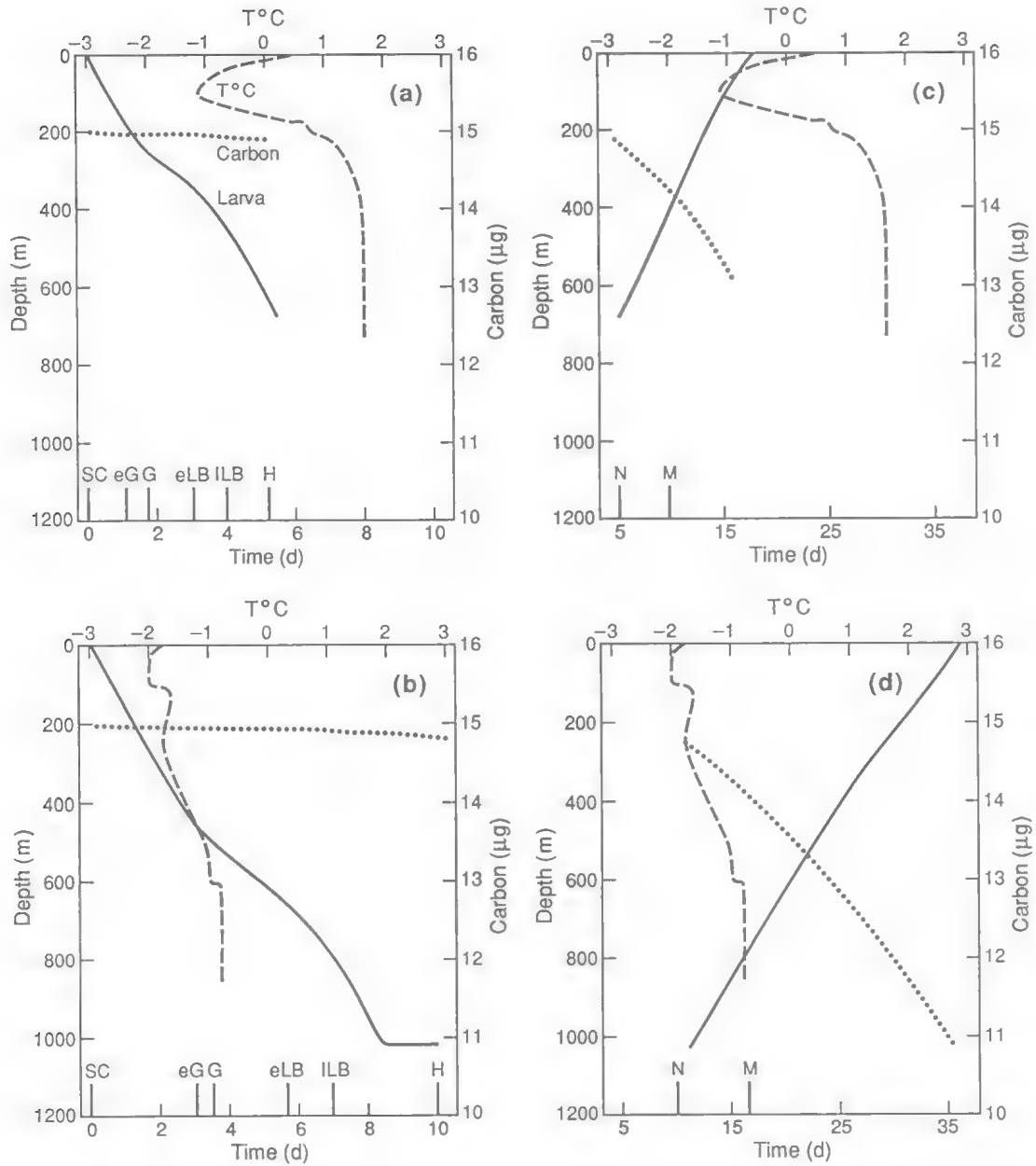


FIG. 2. Simulation of descent/ascent cycle of the embryos and larvae of *Euphausia superba* with vertical temperature structures typical of the region west of the Antarctic Peninsula and north of Anvers Island: temperature profile (dashed line), depth profile (solid line) and carbon content (dotted line) of the embryo or larva. a, descent of embryo, north of King George Island (60.8°S, 58.5°W). b, descent of embryo, eastern Bransfield Strait (63.5°S, 61.4°W). c, ascent of larva, north of King George Island (60.8°S, 58.5°W). d, ascent of larva, eastern Bransfield Strait (63.5°S, 61.4°W). (SC= single cell; eG= early gastrula; G= gastrula; eLB= early limb bud; ILB= late limb bud; H= hatch; N= nauplii; M= metanauplii) (from Hofmann *et al.*, in press).

developing at cold temperatures may spend some of their developmental time on the bottom, where they may be eaten by benthic animals or buried in sediment. Secondly, that larvae which complete the descent/ascent cycle at cold temperatures have less time after reaching the surface to find food before passing the PNR. And lastly, that most of early development in these regions with no CDW takes place at negative temperatures, so the probability is high that the early stages have been exposed to cold temperatures during the temperature sensitive period, and will never develop past C1. Embryos released in regions with CDW at depth will thus encounter more favourable conditions for continued development and maximising the reserves available after reaching the surface.

#### REPRODUCTIVE STRATEGY

Several investigators have suggested that waters over the continental slope, and not shallow waters, are favourable spawning areas because early larval stages are regularly abundant on the continental slope and not on the shelf (Ichii, 1990). In addition gravid females are generally found in areas along the continental slope of the Antarctic Peninsula with high chlorophyll *a* concentrations (Quetin and Ross, 1984b; Endo *et al.*, 1986; Siegel, 1988; Capella *et al.*, in press). The energetic requirements of spawning suggest that food availability is a limiting factor for reproduction (Ross and Quetin, 1986) so the co-occurrence of spawning populations and high food concentrations is not surprising.

Since the spawning distribution of *E. superba* is spatially restricted relative to the distribution of the species, and the distribution of adult krill changes seasonally (Siegel, 1988), the question arises as to whether this spawning distribution is defined by hydrographic conditions as is true of many fishes (Sinclair, 1988). Siegel (1988) suggested that adult krill might actively migrate during summer into offshore waters, and back into shelf waters in the fall. Siegel speculated that this horizontal migration might reduce intraspecific food competition between adults and larvae. The results of the time- and temperature dependent model of the descent-ascent cycle provide an alternate hypothesis: spawning in regions with CDW at depth confers a reproductive advantage on the population and is thus part of a reproductive strategy.

In our study region west of the Antarctic Peninsula and northeast of Anvers Island, most schools of reproducing females are associated with

CDW (Fig. 1 for 1981–82 season; Capella *et al.*, in press). Selection of particular waters by spawning krill cannot be thought of as fortuitous, particularly as the presence of mature females in continental slope waters over CDW appears to involve a seasonal horizontal migration. We suggest that a reproductive strategy has evolved in krill in response to its environment that is composed of at least two elements: the sinking rate pattern of the embryos, and the specific geographic pattern in population structure.

Fisheries scientists first recognised that reproductive strategies, including restricted spawning locations and horizontal migrations, play a definite role in population maintenance and persistence of a species in the late 1800s (Sinclair, 1988). Recently, these restricted distributions have been perceived in several groups of fishes as interactions between reproductive strategies and oceanographic conditions (Parrish *et al.*, 1981; Sherman *et al.*, 1986). The general concept is that the life cycle and structure of the population has evolved in response to specific oceanographic or spatial conditions to take advantage of features in the environment that enhance the survival of the early life history stages (Sinclair, 1988).

In the case of *E. superba*, the hypothesised reproductive strategy confers three advantages. (1) the depth of hatching and time on the bottom is minimised; (2) carbon use before metamorphosis into C1 is minimised, with obvious advantages in increasing the time before passing the PNR; and (3) the embryo and early larvae spend a minimal time in sub-zero waters, where they may be exposed to very cold temperatures during the postulated temperature sensitive period. Recruitment might be affected in several ways if embryos are not released above CDW, as may happen in years when changes in circulation patterns shift the surface distributions of adult krill in summer away from CDW (Capella *et al.*, in press). Mortality of both the larvae and embryos will be increased, because of the temperature sensitive period, deep hatching depths, and greater use of energy reserves. Those larvae that do reach the surface will be less tolerant of subsequent periods of low food availability.

In 1983–84 krill biomass in the study region (Fig. 1) was very low, as documented by the many researchers involved in SIBEX (Second International BIOMASS Experiment). This low biomass has been attributed to large scale population displacement due to hydrographic changes, and not to severe mortality in the adult population or to poor recruitment several years previously (Priddle *et al.*, 1988). The one area

where gravid females were consistently found was the Gerlache Strait (Capella *et al.*, in press). In this year when gravid females were few relative to other years, and not found in the traditional spawning locations over continental slopes and CDW, spawning success as judged by the abundance of the early life history stages was poor (Witek and Kittel, 1985).

#### PHYSIOLOGICAL CONDITION DURING THE FIRST WINTER

The second critical period is during the first winter, when larvae must survive a six-month period of very low food availability in the water column after a brief summer in which to build up energy reserves. Three lines of evidence suggest that low food conditions in the winter may present difficulties for the young-of-the-year who winter over primarily as late furcilia stages or early juveniles (Guzman, 1983; Ross *et al.*, 1987). First, unlike the adults who satisfy a significant portion of their winter energetic requirements with their lipid reserves (Quetin and Ross, 1991), the small amount of lipid accumulated by the larvae is not enough to contribute significantly to energetic requirements. In the fall about 2% of the wet weight of furcilia 6 and juvenile krill is lipid, compared to 6–8% for adults (Quetin and Ross, 1991; unpubl.). Second, furcilia do not have the same starvation capabilities as adults, supporting the evidence of low lipid reserves. Elias (1990) found that the mean survival time of late furcilia under starvation conditions varied with the age of the larvae (Table 1). The older larvae survived longer than younger larvae, but no stage could survive a winter with no food, unlike adults that can starve at least as long as 211 days (Ikeda and Dixon, 1982). Third, when furcilia larvae are maintained at food concentrations representative of the range of winter chlorophyll *a* concentrations in the water column west of the Antarctic Peninsula, larvae at the minimum concentrations ( $0.09 \mu\text{g chl a L}^{-1}$ ) turned to cannibalism while larvae at maximum concentrations ( $0.28 \mu\text{g chl a L}^{-1}$ ) did not (Elias, 1990). The lowest food concentrations appear to have triggered a change in nutritional mode, whether due to a change in behaviour of the larvae or a growing inability of the larvae to escape predation. In the field, however, cannibalism is less likely to occur than in the confined experimental vessels in the laboratory, and larvae may need to find other food sources. These results all suggest that if phytoplankton is the only food source, larvae and early juvenile krill will not

TABLE 1. Starvation tolerance of late furcilia stages of *Euphausia superba*. Larvae were collected in April, and kept at ambient food and temperature for 2.5 months. In July individuals were isolated and maintained in filtered seawater until they died (Elias, 1990).

Stage at Collection	Mean Survival Time (Days)
Furcilia 4	29
Furcilia 5	59
Furcilia 6	54

be able to meet their energetic requirements in open water in the winter when phytoplankton levels are at or near winter minimum concentrations. Their continued development during the winter in the field, inability to tolerate long periods of starvation, and lack of lipid reserves all suggest that larvae need to feed in winter and must utilise a food source other than the phytoplankton in the water column.

Many have speculated about the role of ice and the ice-biota in the winter-over existence of *E. superba* (references in Quetin and Ross, 1991). But quantitative estimates of the importance of the sea ice as either a food source or a refuge from predation, and its impact on recruitment are lacking. We do know, however, that larvae and juveniles feed on the under side of the ice in areas of annual or smooth ice both winter and spring (Guzman, 1983; Kottmeier and Sullivan, 1987; Quetin and Ross, 1988; Daly and Macaulay, 1988; Marschall, 1988). If larval and juvenile krill are dependent on ice-biota in the winter, then their ability to survive the winter in good condition is indirectly dependent on the timing and extent of pack ice development during the winter. We hypothesise that the condition of the larval and juvenile krill and their winter over survival will be higher in years of greater pack ice when food availability is also greater.

Inter-annual variation in the maximum extent of pack ice in the winter is substantial (Zwally *et al.*, 1983; Smith *et al.*, 1988), and can be dramatic in the region west of the Antarctic Peninsula (Quetin and Ross, 1991). Timing is also variable. In some years pack ice is present by July, but in others not until late August. These inter-annual variations in pack ice extent allow us to test predictions based on our hypothesis. The impact of the first winter on recruitment of any one year class into the subadult population will depend on mortality due to either physiological factors or predation. Although quantifying winter-over

survival or recruitment into the subadult population is difficult, we can quantify the physiological parameters that affect survival probabilities. If predation on these young-of-the-year is low, physiological condition and survival should depend on many of the same environmental factors and be well correlated. Because most known predators select the larger size fraction of krill, predation pressure on the furcilia and juveniles will be low (Croxall *et al.*, 1988; Lowry *et al.*, 1988).

#### PHYSIOLOGICAL CONDITION

We define physiological condition as a group of three measurements that depend on the nutritional history of the larva: instantaneous growth rate, condition factor, and lipid content (Quetin *et al.*, in press). Instantaneous growth rate experiments are conducted on board ship for four days immediately after collection (Quetin and Ross, 1991). The brevity of the experiment ensures that these growth rates reflect the immediate previous nutritional history, and are not a laboratory artifact. Condition factor, a measure of organic matter per unit body volume, is more frequently used as an index of nutritional history for fish (Ehrlich *et al.*, 1976), but has occasionally been used for pelagic crustaceans (Omori, 1970; Durbin and Durbin, 1978). Condition factor ( $\mu\text{g}$  carbon per length cubed) is higher under better nutritional conditions. Lipid is commonly used by crustaceans as an energy reserve. Both condition factor and total lipid reflect longer term nutritional history than growth rate. These factors allow us to evaluate the relative

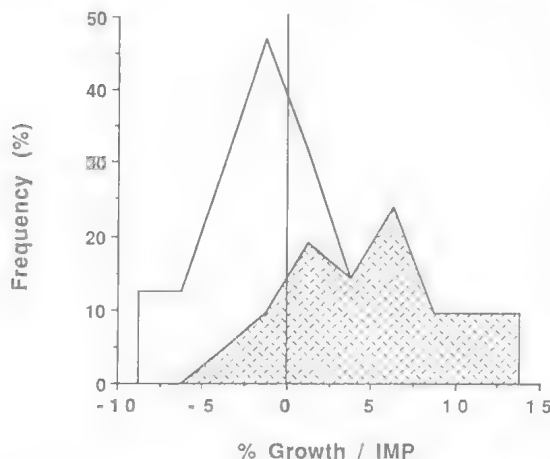


FIG. 3. Distribution of growth increments per intermolt of larvae of *Euphausia superba* in the winters of 1987 (flecked), with heavy pack ice, and 1989 (no fill), with light pack ice. The vertical line is the no-growth line.

'fitness' of the larvae in the field and to distinguish good years from bad.

Physiological condition of larval krill from the region west of the Antarctic Peninsula was measured in two winters that differed greatly in pack ice extent (Quetin *et al.*, in press). Pack ice was heavy in the winter of 1987 (9/10 and 10/10 over most of the region), but nearly non-existent in 1989 (Quetin and Ross, 1991). Other possible significant environmental variables were similar in the two years. Chlorophyll a concentrations in the water column were about  $0.10 \mu\text{g chl a L}^{-1}$  in both years, but temperatures were slightly lower in the heavy ice year ( $-1.6$  to  $-1.8^\circ\text{C}$  versus  $-0.2$  to  $-1.8^\circ\text{C}$ ). Larval krill were collected from open water with paired meter nets on a bongo frame with  $505 \mu\text{m}$  mesh, and by divers from under the ice when ice was present. Stages collected ranged from furcilia 3 to 6 to small juvenile young-of-the-year.

Growth rates were positive in the heavy ice year, but negative in the light ice year (Fig. 3) (Quetin *et al.*, in press). Growth was  $5.43\%$  per intermolt period in the heavy ice year ( $n = 21$ ,  $SD = 4.95$ , 5 experiments), and  $-3.42\%$  per intermolt period in the light ice year ( $n = 8$ ,  $SD = 3.45$ , 3 experiments). Intermolt periods in the winter of light ice were twice those during the winter of heavy ice. Although these longer intermolt periods minimised actual shrinkage per day, growth rates were still zero or negative in winters of low ice.

Condition factor and lipid content were both significantly higher for all larval stages collected during the heavy ice year than during the light ice year (Fig. 4) (Quetin *et al.*, in press). The differences were greater for lipid than for condition factor. Total lipid in larvae from the light ice year was only about half that in the heavy ice year, whereas condition factors differed by about 20%. Thus in the winter of heavy pack ice larvae were in better physiological condition: they were growing, and contained more organic matter per volume and more lipid, some of which could presumably be used to meet energetic demands. Shrinkage, and use of lipid and body protein are all mechanisms used by adult krill to survive a winter of low food availability (Quetin and Ross, 1991). In the light ice year larvae appear to be using some of the same mechanisms to supply their energetic requirements as adults do in all years. However, we know that larvae cannot survive starvation for as long as adults. If very low food concentrations continue for the entire winter, the

larvae will continue to deplete their body lipid and protein, and may pass the PNR. Once past the PNR these larvae will not recruit into the juvenile and subadult population in the late spring and early summer.

Although the mechanisms underlying these correlations are still largely unknown, the difference in physiological condition in larvae from a heavy and a light ice winter suggests that enhancement of winter-over survival is mediated by the presence of pack ice. The most probable cause is the presence of an alternate food source which allows the young-of-the-year to continue to grow and develop throughout the winter without using their body reserves to meet energetic requirements.

#### INTER-ANNUAL VARIABILITY IN RECRUITMENT

Variability in recruitment of a zooplankton population in any one region is caused by a number of factors. The abundance of any one year class is dependent on both the number of embryos actually released and how many of those embryos survive the first year. Spawning intensity in the region varies with the number of reproducing females and the number of embryos each produces. Thus spawning intensity in *E. superba* will depend not only on large scale hydrographic changes that cause regional changes in population structure (Priddle *et al.*, 1988), but also the amount and timing of food availability (Ross and Quetin, 1986). We will term this factor in the recruitment equation 'recruitment potential'. Mortality of the young-of-the-year is the other major factor.

There is evidence for significant inter-annual variability in 'recruitment potential' of *E. superba* in the region west of the Antarctic Peninsula and north of Anvers Island. Brinton *et al.* (1986, 1987) reviewed available information on early larval and gravid female abundance and distribution, and suggested that eight of the twelve years from 1965 to 1984 for which we have information have been successful spawning years for *E. superba*. In the years with poor 'recruitment potential' one or more of the following was observed: gravid females were rare in the area (1982-83; 1983-84); spawning was delayed (1977-78; 1983-84); or larval development was retarded (1966-67). Larval abundance in one of the 'successful' years during this period (1980-81) was much greater than in either 1983-84 (Brinton *et al.*, 1987) or 1976 or 1978 (Hempel, 1985). The 1980-81 year

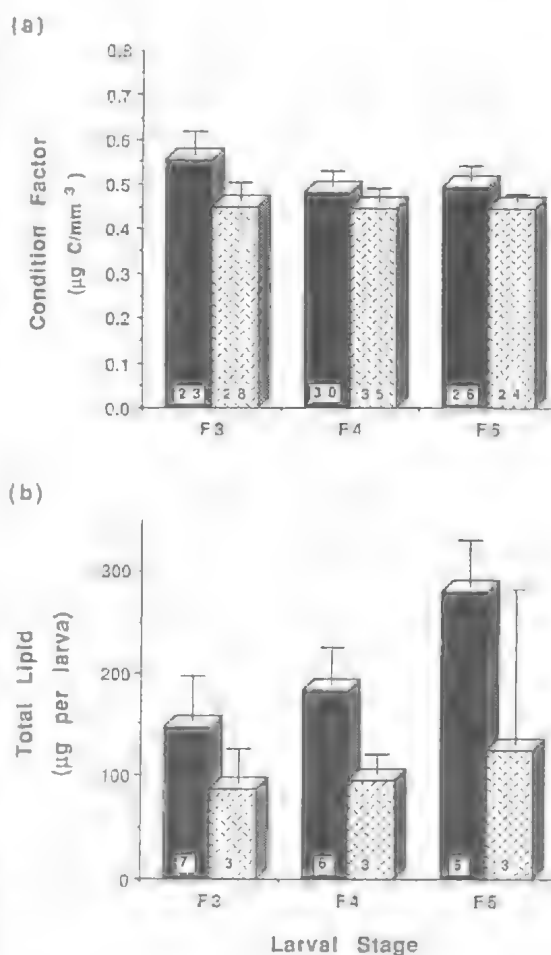


FIG. 4. Condition of the three late furcilia stages of *Euphausia superba* in the winters of 1987 (solid), with heavy pack ice, and 1989 (flecked), with light pack ice. a, condition factor in  $\mu\text{g carbon mm}^{-3}$ . b, total lipid in  $\mu\text{g larva}^{-1}$ . Lipid content of a group of 5 to 8 individuals of the same stage was determined with a charring technique (Marsh and Weinstein, 1966). Error bars represent standard deviations. Numbers in bars are numbers of individuals for condition factor or number of samples of groups of five to eight of the same stage for total lipid.

of high 'recruitment potential' followed a cold winter, as evidenced by extremely cold air temperatures in this region (Rakusa-Suszczewski, 1988) and heavy winter pack ice in the Weddell sector (Zwally *et al.*, 1983) (Fig. 5). The poor 'recruitment potential' years appear to coincide or lag one year behind El Niño Southern Oscillation (ENSO) events (1965-66; 1972-73; 1976-77; 1982-83 (Sahrhage, 1988)) and occur after warmer winters.

Evidence for interannual variability in mortality of the later larval stages is scarce. With a long-lived species such as *E. superba*, only when recruitment fails in several years in succession will we be able to detect differences in absolute abundance (Priddle *et al.*, 1988). However, age-specific differences in mortality rates will lead to predictable changes in length-frequency distributions. For instance, high mortality rates for young-of-the-year in the winter would lead to a length-frequency distribution dominated by older, larger krill the following summer, and low mortality rates to a high-proportion of the population as juveniles or sub-adults. Using such an analysis to separate out the effects of 'recruitment potential' and winter-over survival, however, requires a good estimate of spawning intensity. Siegel (1988) attempted to follow certain year classes from an analysis of the length-frequency distribution of krill catches. Siegel (1988) suggested that larvae from the 1979–80 season were scarce in later years, but larvae from the 1980–81 season were abundant the following year. The first winter for both these year classes, i.e. the winters of 1980 and 1981, was cold with heavy ice pack (Fig. 5). Yet recruitment differed significantly. One possible factor is that mean air temperatures in this region in the winter of 1979 were warmer than usual, and reflect the low ice cover that winter and spring (Zwally *et al.*, 1983). Thus winter and spring conditions were not favourable for 'recruitment potential' in 1979–80, yet were favourable in 1980–81. The year class of 1980–81 had high 'recruitment potential' and probably high winter-over survival.

The existing evidence thus suggests that 'recruitment potential' and winter-over survival both vary from year to year, and that both appear to be correlated with environmental conditions during the winter and early spring. However, a decrease in one is not necessarily followed by a decrease in the other. 'Recruitment potential' reflects environmental conditions before the spawning season, and winter survival reflects conditions the winter after the spawning season.

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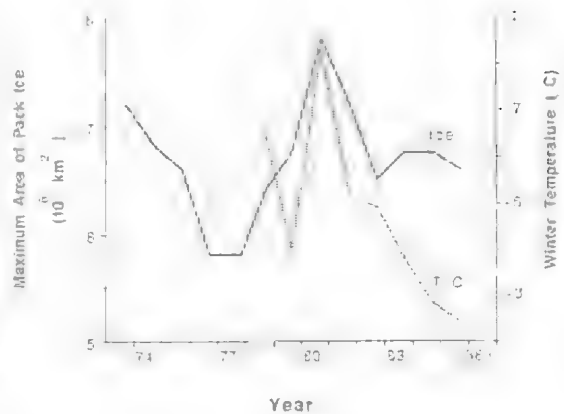


FIG. 5. Maximum extent of pack ice in the Weddell Sea sector (September, October) (Zwally *et al.*, 1983; Smith *et al.*, 1988) and mean winter (June, July, August and September) air temperatures at Admiralty Bay, King George Island (Rakusa-Suszczewski, 1988) from 1973 to 1986.

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